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A Mathematical Model of Population Dynamics with Predator's Behavioral Change Induced by Prey's Batesian Mimicry

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被食者のベイツ型擬態に誘発される捕食者の行動変化を導入した個体群動態モデル

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We analyze a mathematical model of the population dynamics among a mimic, corresponding model, and their predator populations. The predator changes its search-and-attack probability by forming and losing its search image. The predator cannot distinguish the mimic from the model, so that each predator searches and attacks them with common probability. Once a predator predaes a model individual, it comes to omit both the model and the mimic species from its diet menu, and then not to search nor attack them in the same day. If a predator predaes a mimic individual, it comes to increase the search-and-attack probability for both model and mimic. The predator may lose the repulsive/attractive search image with a probability per day. Analyzing our model, we can find the condition for the persistence of model and mimic populations, and then get the result that the condition for the persistence of model population does not depend on the mimic population size, while the condition for the persistence of mimic population does depend on the the predator's ability of the repulsive search image formation.

本研究では、ベイツ型の mimic (擬態) 種とそれに対する model (被擬態) 種、それらに対する捕食者種との間の個体群動態の数理解析モデルを解析した。捕食者における探索像の記憶と忘却により捕食確率が変化する。毎日の捕食活動時間における個体群動態を常微分方程式系で、 T 日間の捕食シーズンの後の生残個体による繁殖を Beverton-Holt 差分方程式モデルで与えて、次の捕食シーズンの初期条件を定めるという過程から成る数理解析モデルを構築し、解析した。model 種と mimic 種は捕食者に同類の餌として認識される。model 個体を捕食した後の捕食者の捕食確率は 0 に、mimic 個体を捕食した後の捕食者の捕食確率はある高レベルに遷移する。捕食者個体群サイズは餌個体群サイズに依存せず、一定であるとする。捕食活動時間終了時の高捕食確率状態にある捕食者の頻度、捕食回避状態にある捕食者の頻度は、捕食履歴 (記憶) の忘却により、翌日までにある一定の割合で減少し、その減少した頻度分により、翌日の中庸な捕食確率状態にある捕食者の初期頻度が定まる。構成された数理解析モデルの解析により、model 個体群の存続条件は、mimic 個体群サイズに依存しないが、mimic 個体群の存続は、捕食者の探索像記憶保持の程度に依存することが示された。

1 Introduction

In this work, we analyze a mathematical model of the population dynamics among a mimic, corresponding model, and their predator populations. The predator changes its search-and-attack probability by forming and losing its search image. We analyze a mathematical model consisting of the daily population dynamics with ordinary differential equations, the seasonal population dynamics with difference equations, and the annual population dynamics with difference equations.

The predator cannot distinguish the mimic from the model, so that each predator searches and attacks them with common probability. Once a predator predaes a model individual, it comes to omit both the model and the mimic species from its diet menu, and then not to search nor attack them in the same day. If a predator predaes a mimic individual, it comes to increase the search and attack probability for the model and the mimic. The predator population size is assumed to be kept constant, independently of the model and the mimic population sizes. The frequency of predators with higher search-and-attack probability and that with zero search-and-attack probability decreases by a rate between the subsequent days, because of the predator's losing the search image. Analyzing our model system, we can get the result such that the condition for the persistence of model population does not depend on the mimic population size, while the condition for the persistence of mimic population does depend on the predator's ability of the search image formation.

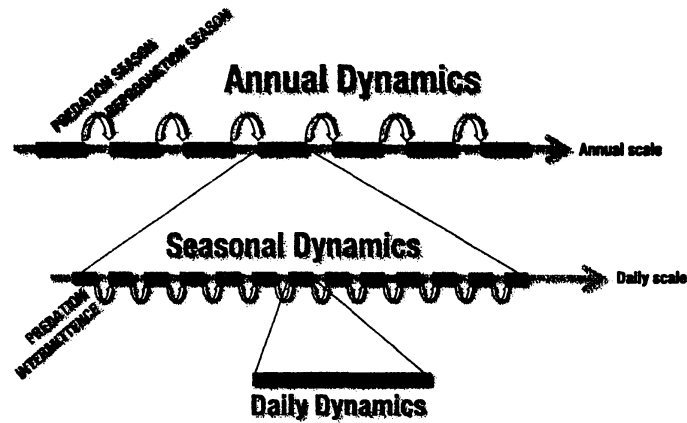


Figure 1: Multi time-scale structure of population dynamics in our model.

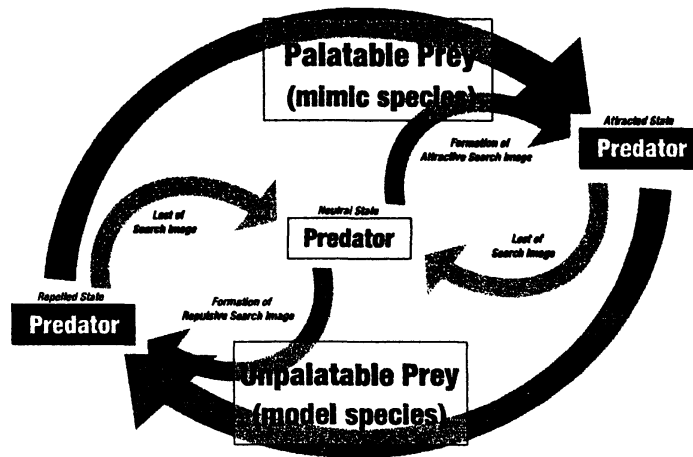


Figure 2: Pradator's state transition due to predating the model or the mimic prey.

2 Model

We analyze a mathematical model consisting of the daily population dynamics with ordinary differential equations, the seasonal population dynamics with difference equations, and the annual population dynamics with difference equations (see Fig. 1). Each predation season is composed with the daily dynamics repeated day by day in T days.

The predator population size is assumed to be kept constant, given by P , independently of the model and the mimic population sizes. This means such an assumption that the predator is a generalist and has some other preys to keep the stationary population size, so that it can survive and sustain its population even if the model and the mimic population go extinct.

The reproductions of model, mimic, and predator species is assumed to occur between the subsequent predation seasons. In other words, there is no reproduction of model, mimic or predator within the predation season, so that the model and the mimic populations monotonically decrease due to the predation during the predation season.

Daily dynamics

The predator cannot distinguish the mimic from the model, so that each predator searches and attacks them with common probability. Once a predator predaes a model individual, it comes to omit both the model and the mimic species from its diet menu, and then not to search nor attack them in the same day. If a predator predaes a mimic individual, it comes to increase the search-and-attack probability for both the model and the mimic (see Fig. 2).

At the predation period in the k th day of predation season, the predator subpopulation without any search image for the model/mimic prey is now given by $P_k^0(t)$ ($k = 1, 2, \dots, T$), at time t after the beginning of the predation period ($t = 0$). In the same way, the predator subpopulation with higher search-and-attack probability after predating a mimic prey is given by $P_k^+(t)$, and that with zero probability after predating a model prey by $P_k^-(t)$. From the assumption of a constant predator population size,

$$P_k^0(t) + P_k^+(t) + P_k^-(t) = P$$

for any $t \in [0, \tau]$, where τ is the length of predation period in which the daily dynamics undergoes in each day. The model and the mimic population sizes at time $t \in [0, \tau]$ in the daily dynamics are given by $m_k(t)$ and $x_k(t)$.

In our model, the daily dynamics is governed by the following ordinary differential equations:

$$\begin{aligned} \frac{dm_k(t)}{dt} &= -F_M^0 P_k^0(t) - F_M^+ P_k^+(t); \\ \frac{dx_k(t)}{dt} &= -F_X^0 P_k^0(t) - F_X^+ P_k^+(t); \\ \frac{dP_k^0(t)}{dt} &= -F_M^0 P_k^0(t) - F_X^0 P_k^0(t); \\ \frac{dP_k^+(t)}{dt} &= F_X^0 P_k^0(t) - F_M^+ P_k^+(t); \\ \frac{dP_k^-(t)}{dt} &= F_M^0 P_k^0(t) + F_M^+ P_k^+(t), \end{aligned} \tag{1}$$

where F_M^0 is the predation rate for the model per unit population size of $P_k^0(t)$ at time t , and the others are defined as well, which are now given by

$$\begin{aligned} F_M^0 &= \mu_k(t) \cdot b_0 \{m_k(t) + x_k(t)\}; & F_M^+ &= \mu_k(t) \cdot \frac{b_0}{c^+} \{m_k(t) + x_k(t)\}; \\ F_X^0 &= \chi_k(t) \cdot b_0 \{m_k(t) + x_k(t)\}; & F_X^+ &= \chi_k(t) \cdot \frac{b_0}{c^+} \{m_k(t) + x_k(t)\} \end{aligned}$$

with

$$\mu_k(t) = \frac{m_k(t)}{m_k(t) + x_k(t)}; \quad \chi_k(t) = \frac{x_k(t)}{m_k(t) + x_k(t)}.$$

Parameter b_0 is the predation coefficient of the predator which does not experience the predation of the model and the mimic preys. The contact rate of a predator with preys is assumed to be proportional to the sum of model and mimic populations, $m_k(t) + x_k(t)$. Parameter c^+ is positive and less than 1, which gives the increase of predation rate by the creation of search image due to the predation of the mimic prey.

Making use of the following non-dimensionalizing parameter transformation:

$$b_0 t \rightarrow t; \quad b_0 \tau \rightarrow \tau; \quad \frac{P_k^0(t)}{P} \rightarrow p_k^0(t); \quad \frac{P_k^+(t)}{P} \rightarrow p_k^+(t); \quad \frac{P_k^-(t)}{P} \rightarrow p_k^-(t),$$

the system (1) becomes

$$\begin{aligned}
\frac{dm_k(t)}{dt} &= -P \left\{ p_k^0(t) + \frac{p_k^+(t)}{c^+} \right\} m_k(t); \\
\frac{dx_k(t)}{dt} &= -P \left\{ p_k^0(t) + \frac{p_k^+(t)}{c^+} \right\} x_k(t); \\
\frac{dp_k^0(t)}{dt} &= -\{m_k(t) + x_k(t)\} p_k^0(t); \\
\frac{dp_k^+(t)}{dt} &= p_k^0(t)x_k(t) - \frac{p_k^+(t)}{c^+} m_k(t); \\
\frac{dp_k^-(t)}{dt} &= \left\{ p_k^0(t) + \frac{p_k^+(t)}{c^+} \right\} m_k(t).
\end{aligned} \tag{2}$$

Now p_k^0 , p_k^+ and p_k^- respectively mean the frequency of predators according to the state characterized by the search-and-attack probability, satisfying that

$$p_k^0(t) + p_k^+(t) + p_k^-(t) = 1$$

for any $t \in [0, \tau]$.

Seasonal dynamics

The model and the mimic population sizes at the end of k th predation period in the predation season are given by $m_k(\tau)$ and $x_k(\tau)$. They give the initial population sizes in the subsequent predation period of the next day: $(m_{k+1}(0), x_{k+1}(0)) = (m_k(\tau), x_k(\tau))$. We ignore the death rate due to any other reasons except for the predation in every day of the predation season.

As for the frequencies in the predator population, we introduce the probability of losing the search image, say, the forgetting probability. The predator loses its search image with a probability between the end of a predation period and the beginning of the subsequent predation period. The predator with the higher search-and-attack probability loses it with probability $1 - \sigma^+$, where σ^+ means the probability to keep the attractive search image ($0 \leq \sigma^+ \leq 1$). The predator with the lower search-and-attack probability loses it with probability $1 - \sigma^-$ ($0 \leq \sigma^- \leq 1$). So the parameter σ^- means the probability to keep the repulsive search image. Therefore, we assume the relation between the predator frequencies at the end of k th predation period and those at the beginning of $k + 1$ th one as follows:

$$\begin{aligned}
p_{k+1}^0(0) &= p_k^0(\tau) + (1 - \sigma^+)p_k^+(\tau) + (1 - \sigma^-)p_k^-(\tau); \\
p_{k+1}^+(0) &= \sigma^+ p_k^+(\tau); \\
p_{k+1}^-(0) &= \sigma^- p_k^-(\tau).
\end{aligned} \tag{3}$$

Hence, if the model and the mimic populations do not exist or goes extinct, the frequency p^0 asymptotically approaches 1 day by day in a geometric manner. These boundary conditions for the model/mimic populations and the predator frequencies govern their seasonal dynamics through each predation season of T days.

Annual dynamics

Let us consider the n th predation season. The initial population sizes of model and mimic are given by $m_1(0)$ and $x_1(0)$ from the definitions for the daily dynamics. These initial population sizes simultaneously define the initial population sizes for the n th predation season, now rewritten by $M_{n,0}$ ($= m_1(0)$) and $X_{n,0}$ ($= x_1(0)$).

In our model, the reproduction of the model and the mimic populations is given by what is called Beverton–Holt model. Since the reproduction season is now assumed to be between subsequent predation seasons, their population sizes $(m_T(\tau), x_T(\tau))$ at the end of n th predation season determine

$(M_{n+1,0}, X_{n+1,0}) = (m_1(0), x_1(0))$ at the beginning of $n + 1$ th predation season:

$$\begin{aligned} M_{n+1,0} &= \frac{r_M m_T(\tau)}{1 + \beta_M m_T(\tau)}; \\ X_{n+1,0} &= \frac{r_X x_T(\tau)}{1 + \beta_X x_T(\tau)}, \end{aligned} \quad (4)$$

where r_M and r_X are respectively the intrinsic growth rate, β_M and β_X the density effect coefficient.

In our model, we assume that the predator completely loses the search image in the period between subsequent predation seasons. Thus the initial condition for the predator's frequencies according to the state of search-and-attack probability is given by

$$(p_1^0(0), p_1^+(0), p_1^-(0)) = (1, 0, 0),$$

on the first day of any predation season, independently of their values at the end of previous season.

3 Analysis

Daily dynamics

From (2), we can easily find that $d(\log m_k)/dt = d(\log x_k)/dt$ for any $t \in [0, \tau]$. This means that the ratio $x_k(t)/m_k(t)$ is constant independently of t , so that $x_k(t)/m_k(t) = x_k(0)/m_k(0)$ for any $t \in [0, \tau]$ and any $k = 1, 2, \dots, T$. Moreover, from the boundary condition $(m_{k+1}(0), x_{k+1}(0)) = (m_k(\tau), x_k(\tau))$, we lastly have

$$\frac{x_k(t)}{m_k(t)} = \frac{x_k(0)}{m_k(0)} = u_n := \frac{x_1(0)}{m_1(0)} \quad (5)$$

for any $t \in [0, \tau]$ and any $k = 1, 2, \dots, T$ in the n th predation season. We remark that, from the definition, $x_1(0)/m_1(0) = M_{n,0}/X_{n,0}$, the ratio at the beginning of the first predation period in the n th predation season. Furthermore, from (2), we can find that $d(m_k + p_k^- P)/dt = 0$ for any $t \in [0, \tau]$, too. Thus, we have

$$m_k(t) = m_k(0) - \{p_k^-(t) - p_k^-(0)\}P \quad (6)$$

for any $t \in [0, \tau]$.

Now, from (2), since $dm_k/dt < 0$ for any $p_k^0 > 0$, $p_k^+ > 0$ and $m_k > 0$, $m_k(t)$ is monotonically decreasing in terms of $t \geq 0$. On the other hand, $m_k(t) \equiv 0$ is a specific solution for the first differential equation of (2). Thus, because of the uniqueness of solution, $m_k(t)$ with any positive initial value $m_k(0) > 0$ is bounded from below. Therefore, $\lim_{t \rightarrow \infty} m_k(t) = m_k^* \geq 0$ exists. From (2) with the trivial boundedness such that $p^- \leq 1$, making use of the analogous arguments, we find that $\lim_{t \rightarrow \infty} p_k^-(t) = p_k^{-*} \geq 0$ exists, too. Lastly, this means that $\lim_{t \rightarrow \infty} p_k^+(t) = p_k^{+*} \geq 0$ and $\lim_{t \rightarrow \infty} p_k^0(t) = p_k^{0*} \geq 0$ exist at the same time.

If $m_k^* > 0$, then, from (2), it is necessary that $p_k^{0*} = p_k^{+*} = 0$ so that $p_k^{-*} = 1$. In this case, from (6), $m_k^* = m_k(0) - \{1 - p_k^-(0)\}P$, which is valid when and only when $m_k(0) > \{1 - p_k^-(0)\}P$. In contrast, from (6), if $m_k^* = 0$, then $p_k^{-*} = p_k^-(0) + m_k(0)/P$ which is valid when and only when $p_k^-(0) + m_k(0)/P \leq 1$, that is, $m_k(0) \leq \{1 - p_k^-(0)\}P$. In this case, from (5), $\lim_{t \rightarrow \infty} x_k(t) = x_k^* = 0$ as well.

With these arguments, now we have the following result:

In the daily dynamics given by (2), the system asymptotically approaches the equilibrium state given by

$$(m_k(t), x_k(t), p_k^0(t), p_k^+(t), p_k^-(t)) \xrightarrow{t \rightarrow \infty} \begin{cases} E_0(0, 0, p_k^{0*}, p_k^{+*}, p_k^{-*}) & \text{if } m_k(0) \leq \{1 - p_k^-(0)\}P; \\ E_+(m_k^*, u_n m_k^*, 0, 0, 1) & \text{if } m_k(0) > \{1 - p_k^-(0)\}P \end{cases} \quad (7)$$

for $k \geq 1$.

Equilibrium state approximation

Now, we introduce an approximation for the state at the end of predation period. Let us assume that the state $(m_k(t), x_k(t), p_k^0(t), p_k^+(t), p_k^-(t))$ approaches the equilibrium state given by (7) sufficiently fast. In other words, we assume that the state at the end of predation period $(m_k(\tau), x_k(\tau), p_k^0(\tau), p_k^+(\tau), p_k^-(\tau))$ is sufficiently near the equilibrium state given by (7). Thus, as an approximation, we hereafter use the equilibrium state given by (7) as the state at the end of predation period.

With this approximation, we reset up the relation between the predator frequencies at the end of k th predation period and those at the beginning of $k + 1$ th one as follows ($k \geq 1$):

$$\begin{aligned} p_{k+1}^0(0) &= \lim_{t \rightarrow \infty} \{p_k^0(t) + (1 - \sigma^+)p_k^+(t) + (1 - \sigma^-)p_k^-(t)\}; \\ p_{k+1}^+(0) &= \lim_{t \rightarrow \infty} \{\sigma^+ p_k^+(t)\}; \\ p_{k+1}^-(0) &= \lim_{t \rightarrow \infty} \{\sigma^- p_k^-(t)\}, \end{aligned} \quad (8)$$

instead of (3).

From (7) and (8), as far as the mimic population persists and the system asymptotically approaches the equilibrium state E_+ in the k th predation period, we have

$$(p_{k+1}^0(0), p_{k+1}^+(0), p_{k+1}^-(0)) = (1 - \sigma^-, 0, \sigma^-).$$

In contrast, once the mimic population goes extinct in the k th predation period with the equilibrium state E_0 in (7), which could be regarded as the consequence of predator's overgrazing, we have

$$\begin{aligned} p_{k+1}^0(0) &= p_k^{0*} + (1 - \sigma^+)p_k^{+*} + (1 - \sigma^-)p_k^{-*}; \\ p_{k+1}^+(0) &= \sigma^+ p_k^{+*}; \\ p_{k+1}^-(0) &= \sigma^- p_k^{-*}. \end{aligned}$$

Subsequently, since the mimic and the model populations have gone extinct, the system (2) gives no change of the predator frequencies in the subsequent predation period. Thus, we have

$$\begin{aligned} p_{k+1}^{0*} &= p_k^{0*} + (1 - \sigma^+)p_k^{+*} + (1 - \sigma^-)p_k^{-*}; \\ p_{k+1}^{+*} &= \sigma^+ p_k^{+*}; \\ p_{k+1}^{-*} &= \sigma^- p_k^{-*}. \end{aligned}$$

Therefore, the predator frequencies geometrically approach $(1, 0, 0)$ day by day after the extinction of the mimic and the model populations, because of the predator's losing the search image.

Now, suppose that the mimic population persists till the k th predation period. Then, from the above arguments, we have $(p_k^0(0), p_k^+(0), p_k^-(0)) = (1 - \sigma^-, 0, \sigma^-)$ for $k > 1$. Further, from (2) and (5), we find that

$$\frac{d}{dp_k^0(t)} \left[\frac{p_k^+(t)}{\{p_k^0(t)\}^{\alpha_n}} \right] = -\frac{u_n}{1 + u_n} \frac{1}{\{p_k^0(t)\}^{\alpha_n}},$$

where $\alpha_n := 1/\{c^+(1 + u_n)\}$. Hence, we can obtain the following relation between $p_k^0(t)$ and $p_k^+(t)$ in the k th predation period:

$$p_k^+(t) = \begin{cases} -(1 - c^+)p_k^0(t) \log \frac{p_k^0(t)}{p_k^0(0)} & \text{if } \alpha_n = 1; \\ \frac{1}{\alpha_n - 1} \frac{u_n}{1 + u_n} p_k^0(t) \left[1 - \left\{ \frac{p_k^0(t)}{p_k^0(0)} \right\}^{\alpha_n - 1} \right] & \text{if } \alpha_n \neq 1. \end{cases}$$

Making use of this equation with $p_k^+(t) = 1 - p_k^-(t) - p_k^0(t)$ and $p_k^{+*} = 1 - p_k^{-*} - p_k^{0*}$, we can easily prove that the equilibrium state E_0 in (7) uniquely exists with $0 < p_k^{0*} < 1$, $0 < p_k^{+*} < 1$ and $0 < p_k^{-*} < 1$.

From these arguments and (7), we can get the following result:

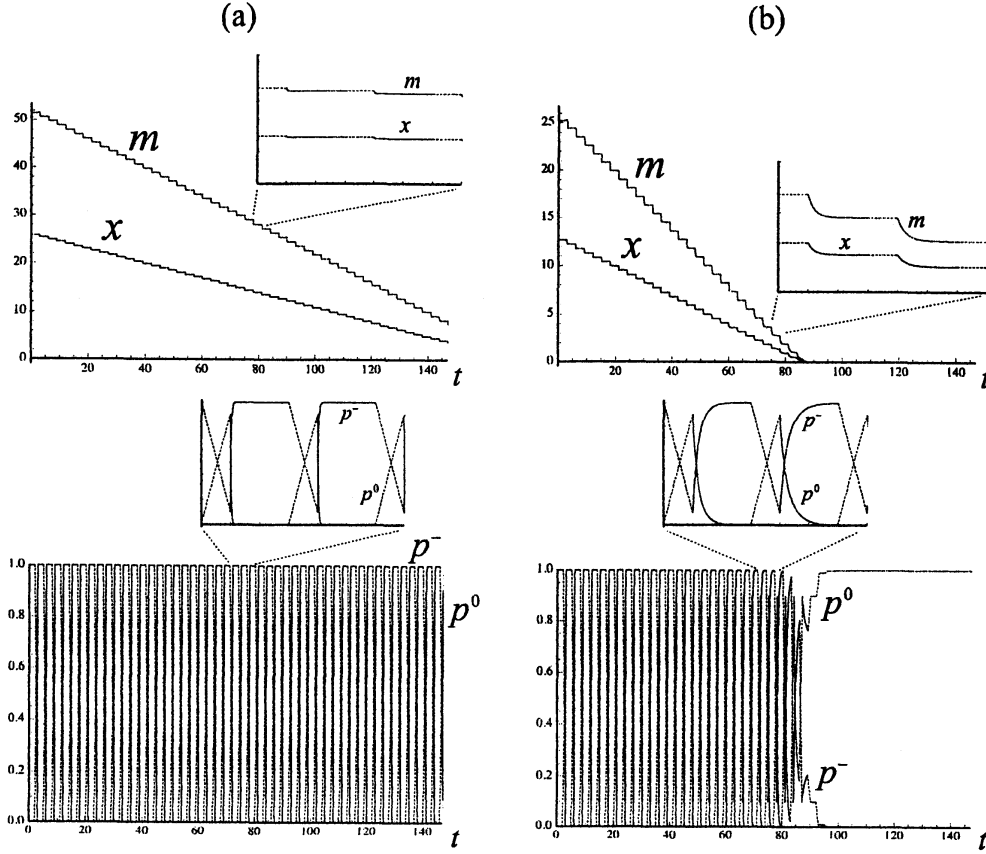


Figure 3: A numerical example of the seasonal dynamics governed by (2) with the equilibrium state approximation (8). Solid curves show the daily dynamics, and dashed curves do the interval between subsequent predation periods. (a) $(m_1(0), x_1(0)) = (52.4469, 26.2234)$; (b) $(m_1(0), x_1(0)) = (26.2234, 13.1117)$. Commonly, $T = 50$, $\tau = 2.0$, $c^+ = 0.1$, $\sigma^+ = 0.5$, $\sigma^- = 0.1$, $P = 1.0$, $m_c = 45.1$. The mimic and the model populations persist through the predation season in (a), while they go extinct on a day of it in (b).

The mimic and the model populations persist in the k th predation period if and only if $m_k(0) > (1 - \sigma^-)P$ for $k > 1$ and $m_1(0) > P$. Then, $(p_k^{0*}, p_k^{+*}, p_k^{-*}) = (0, 0, 1)$ and $m_k^* = m_k(0) - (1 - \sigma^-)P$. for $k > 1$ and $m_1^* = m_1(0) - P$. If and only if $m_k(0) \leq (1 - \sigma^-)P$ for some $k > 1$ or $m_1(0) \leq P$, the mimic and the model populations go extinct in the k th or the first predation period, and then the system approaches the equilibrium state E_0 with $0 < p_k^{0*} < 1$, $0 < p_k^{+*} < 1$ and $0 < p_k^{-*} < 1$.

As for a special case without the model population, when the system contains the mimic and the predator, we can easily shown that the mimic population goes extinct on the first day of predation season with the equilibrium state approximation without the model population .

Seasonal dynamics

Let us consider the case that the mimic and the model populations persist till the k th predation period ($k > 1$). Then, from the above arguments with the equilibrium state approximation, we have the following daily recurrence relation about the initial model population size:

$$m_{j+1}(0) = m_j(0) - \{1 - p_j^-(0)\}P \quad (9)$$

for $j = 1, 2, \dots, k-1$. Since $p_1^-(0) = 0$ and $p_j^-(0) = \sigma^-$ for $j > 1$, this recurrence relation gives the following general form of $m_j(0)$:

$$m_j(0) = m_1(0) - \{1 + (j-2)(1-\sigma^-)\}P \text{ for } j = 2, 3, \dots, k. \quad (10)$$

As a consequence, since the necessary and sufficient condition that the mimic and the model populations persist in the T th predation period (= the last predation period in the predation season) is given by $m_T(0) > (1-\sigma^-)P$ from the result in the previous section, we have the following result about the seasonal dynamics:

The mimic and the model populations persist through the n th predation season if and only if

$$m_1(0) = M_{n,0} > m_c := \{1 + (T-1)(1-\sigma^-)\}P. \quad (11)$$

Otherwise, the mimic and the model populations simultaneously go extinct in the k_e th day of the n th predation season, where the day k_e the extinction occurs is determined by

$$k_e = \min\{j \mid j \geq \frac{M_{n,0}/P - 1}{1 - \sigma^-} + 1, 1 \leq j \leq T\}. \quad (12)$$

In the case that the mimic and the model populations persist through the n th predation season, the mimic population size m_T^* at the end of the predation season is given by

$$\begin{aligned} m_T^* &= m_T(0) - (1-\sigma^-)P = m_1(0) - \{1 + (T-1)(1-\sigma^-)\}P \\ &= M_{n,0} - m_c. \end{aligned} \quad (13)$$

As a consequence, the extinction of only one of mimic and model never occurs in the seasonal dynamics of our model with the equilibrium state approximation, while it is likely that both of them go extinct in it. A numerical example of the seasonal dynamics governed by (2) with the equilibrium state approximation (8) is given in Fig. 3.

Annual dynamics

From (4) with the equilibrium state approximation (8), the model and the mimic populations at the beginning of $n+1$ th predation season, $M_{n+1,0}$ and $X_{n+1,0}$, are now given by the following reproduction functions:

$$\begin{aligned} M_{n+1,0} &= \frac{r_M m_T^*}{1 + \beta_M m_T^*}, \\ X_{n+1,0} &= \frac{r_X x_T^*}{1 + \beta_X x_T^*}, \end{aligned} \quad (14)$$

where

$$x_T^* = u_n m_T^* = \frac{x_1(0)}{m_1(0)} m_T^* = \frac{X_{n,0}}{M_{n,0}} m_T^*$$

from (5). Then, from (7), (11), (13) and (14), we have the following difference equations to determine the annual dynamics in terms of the model and the mimic population sizes at the beginning of predation season:

$$\begin{aligned} M_{n+1,0} &= \frac{r_M [M_{n,0} - m_c]_+}{1 + \beta_M [M_{n,0} - m_c]_+}, \\ X_{n+1,0} &= \frac{r_X [M_{n,0} - m_c]_+ X_{n,0}}{M_{n,0} + \beta_X [M_{n,0} - m_c]_+ X_{n,0}}, \end{aligned} \quad (15)$$

where the symbol $[]_+$ is defined by

$$[x]_+ := \begin{cases} x & \text{for } x > 0; \\ 0 & \text{for } x \leq 0. \end{cases}$$

We note that the annual dynamics of model population is independent of that of mimic population, while the latter depends on the former.

Analyzing the first equation of (15), we can obtain the following result about the persistence of model population:

If and only if the following conditions are satisfied, the model population persists in any predation season, and $M_{n,0} \rightarrow M^ = m_c + \lambda_+ = (r_M - 1 - m_c/\lambda_+)/\beta_M$ as $n \rightarrow \infty$:*

$$r_M \geq (1 + \sqrt{\beta_M m_c})^2; \quad (16)$$

$$M_{1,0} \geq m_c + \lambda_- = (r_M - 1 - m_c/\lambda_-)/\beta_M, \quad (17)$$

where

$$\lambda_{\pm} = \frac{1}{2\beta_M} \left[r_M - (1 + \beta_M m_c) \pm \sqrt{\left\{ r_M - (1 + \sqrt{\beta_M m_c})^2 \right\} \left\{ r_M - (1 - \sqrt{\beta_M m_c})^2 \right\}} \right]. \quad (18)$$

Otherwise, the model population goes extinct in the n_e th predation season with $M_{n_e,0} \leq m_c$, where

$$n_e = 1 + \left\lceil \frac{\log \left(\frac{1 - [M_{n_e,0} - m_c]_+ / \lambda_+}{1 - [M_{n_e,0} - m_c]_+ / \lambda_-} \right)}{\log \left(\frac{1 + \beta_M \lambda_+}{1 + \beta_M \lambda_-} \right)} \right\rceil. \quad (19)$$

The symbol $\lceil x \rceil$ means the smallest integer not less than x .

As for the mimic population governed by the second difference equation of (15), here let us consider it with $M_{n,0} \equiv M^* = m_c + \lambda_+$ for any n . This is because the model population dynamics is independent of the mimic one. Besides, as we have already seen, if the model population goes extinct, then so does the mimic population. Further, we can prove that, even if the mimicry is absent, the seasonal and the annual dynamics for the model population is the same as shown above. So we now focus the mimic population dynamics when the model population has reached its equilibrium state according to the annual dynamics governed by the first difference equation of (15). Hence, instead of the second difference equation of (15), let us consider here the following annual dynamics of mimic population:

$$X_{n+1,0} = \frac{r_X X_{n,0}}{1 + m_c/\lambda_+ + \beta_X X_{n,0}}. \quad (20)$$

From this difference equation, we obtain the following result about the persistence of mimic population:

If and only if the following condition is satisfied when the model population persists at its equilibrium state, the mimic population persists in any predation season:

$$r_X > 1 + \frac{m_c}{\lambda_+} = r_M - \beta_M M^*, \quad (21)$$

and then

$$X_{n,0} \rightarrow X^* = \frac{1}{\beta_X} \left\{ r_X - \left(1 + \frac{m_c}{\lambda_+} \right) \right\} = \frac{\beta_M}{\beta_X} M^* + \frac{r_X - r_M}{\beta_X} \quad (22)$$

as $n \rightarrow \infty$. Otherwise, the mimic population goes extinct, that is, $X_{n,0} \rightarrow 0$ as $n \rightarrow \infty$ for any $X_{1,0} > 0$.

Differently from the case of model population, there is no condition for the initial value $X_{1,0}$ about the mimic population persistence.

We note that, in this result, unless the condition (21) is satisfied, the mimic population tends to go extinct, though its extinction never occurs at any finite time as long as the model population persists. As already seen in the seasonal dynamics, the mimic population goes extinct in a predation season only when so does the model population. Thus, the mimic's extinction in the above result means the tendency for the mimic population to go extinct. In such case, the mimic population size decreases not only day by day in the predation season but also year by year, independently of the temporal variation of model population size.

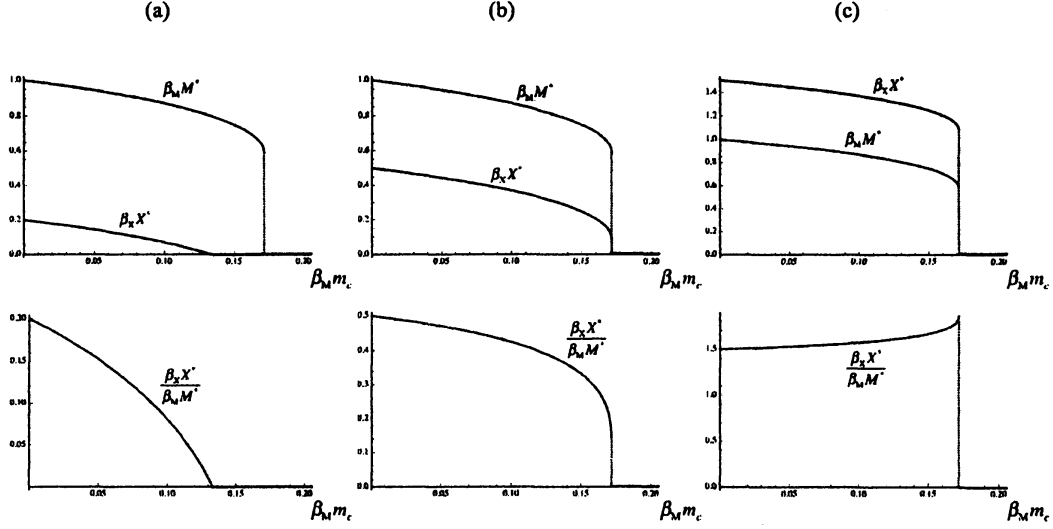


Figure 4: m_c -dependence of equilibrium population sizes at the beginning of predation season, that is, for the annual dynamics of (2) and (14) with the equilibrium state approximation (8). (a) $r_X = 1.2$; (b) $r_X = 1.5$; (c) $r_X = 2.5$. Commonly, $r_M = 2.0$. In case of (a), the mimic population is extinct for a range of m_c in which the model population is persistent. In cases of (b) and (c), the mimic population is persistent as long as the model population is.

Equilibrium population size ratio

In the case when the model population is persistent under those conditions (16) and (17), then, from (5), we can show that the ratio of their population sizes approaches a constant at any moment in the daily dynamics of any predation season:

$$\frac{X_{n,0}}{M_{n,0}} = \frac{x_k(t)}{m_k(t)} = u_n \rightarrow \frac{X^*}{M^*} = \frac{\beta_M}{\beta_X} \cdot \frac{[r_X - 1 - m_c/\lambda_+]_+}{r_M - 1 - m_c/\lambda_+} \quad (23)$$

as $n \rightarrow \infty$, where $[\]_+$ is defined as before. Numerical examples of m_c -dependence of the equilibrium population size ratio are given in Fig. 4.

We can easily find that m_c/λ_+ is monotonically increasing and $m_c + \lambda_+$ is monotonically decreasing in terms of m_c . Since m_c defined in (11) is monotonically decreasing between its minimum P and maximum TP in terms of σ^- , the results of our analysis indicate that the persistence of model and mimic population depends on the predator's ability of repulsive search image formation. Moreover, it is likely that the predator's ability of repulsive search image formation could determine the population size ratio between the mimic and the model populations.

4 Concluding Remarks

As the predator's ability of repulsive search image formation is better, it is more likely for the model population to persist, and the equilibrium model population size gets larger. This is because the better ability of repulsive search image formation indicates to repel the predator from the model population so as to make the predation pressure weaker for it. This feature according to the predator's ability of repulsive search image formation can be adopted to the persistence and the equilibrium size of mimic population, too. At the same time, this result implies that the equilibrium population size ratio between the model and the mimic is affected by the predator's ability of repulsive search image formation.

Beyond these results in the population dynamical nature, we could extend our result to some discussions on the evolution or the invasion of mimicry from the viewpoint of coexistence of the mimic and the model populations. Further, we could discuss the possible coevolutionary relation between the predator and the model/mimic species. We separately show these discussions elsewhere.